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1 **Long-term changes in the total egg production of Norwegian**  
 2 **spring-spawning herring *Clupea harengus* (L.) –**  
 3 **implications of variations in population structure and**  
 4 **condition factor**

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## ABSTRACT

The reproductive potential of Norwegian spring-spawning herring (*Clupea harengus*) was estimated in terms of total egg production (TEP) for the period 1935-2005, using a model where spawning stock numbers (SSN)-, weight- and length-at-age were combined with fecundity-weight relationships. In general, the modelled TEP was closely related to SSN. However, larger positive and negative deviations from this relationship were found in periods with high SSN in combination with increasing proportions of either recruit or repeat spawners and condition factor (K) below 0.73 or above 0.8. When relating the current estimated TEP to similar type of figures based on earlier data (including fecundity observations in 1951-1983), deviations were less pronounced, but they still tended to occur in periods of high SSN. These results suggest that at stable high stock levels, the population structure of the stock and its condition in terms of K, can have implications for the reproductive output. Hence, quantification of the reproductive potential as TEP has the potential to strengthen the stock-recruitment models, because it captures both the stock population structure and reproductive dynamics.

**Keywords:** Norwegian spring-spawning herring, Fecundity, Total egg production, Reproductive potential, Stock recovery

## 1. Introduction

The Norwegian spring-spawning (NSS) herring (*Clupea harengus*) stock is distributed in both the Norwegian and Barents Sea (Holst et al., 2004). Over the past century this commercially valuable stock has undergone substantial fluctuations in abundance and recruitment (Dragesund et al., 1997; Toresen and Østvedt, 2000; Nakken, 2008). In the 1940s the spawning stock was 10 to 16 million tonnes, but it then declined and collapsed in the late 1960s (ICES, 1999; Toresen and Østvedt, 2000, 2002). The lowest estimated spawning stock biomass (SSB) of a few thousand tonnes occurred in 1972, remaining extremely low throughout the 1970s. After implementation of very strict management regulations and a strong year-class in 1983,

the biomass increased, and by 1986, the SSB started recovering, with the current SSB between 8 and 10 million tonnes (ICES, 2007).

SSB has often been used as a proxy for the egg production of a fish population (Trippel, 1999). However, it has become apparent that other factors such as stock age or size structure and individual fish condition can have a considerable influence on the stock reproductive potential (SRP) and this in turn could contribute to the recruitment variability (Marshall et al., 1998, 2000; Trippel, 1998, 1999).

The estimation of SRP is generally undertaken by scaling up from individual level characteristics to population level. Therefore, information is needed on factors influencing the reproductive investment of each fish. Fecundity of NSS herring has been studied both experimentally and in the field, and condition factor was found to have a significant positive effect on oocyte production (Ma et al., 1998; Óskarsson et al., 2002; Kurita et al., 2003; González-Vasallo, 2006). This has also been noted in both marine and freshwater fish species for example, cod (*Gadus morhua*) (Kjesbu et al., 1991; Lambert and Dutil, 2000); haddock (*Melanogrammus aeglefinus*) (Hislop et al., 1978); winter flounder (*Pseudopleuronectes americanus*) (Tyler and Dunn, 1976), brown trout (*Salmo trutta*) (Bagenal, 1969) and rainbow trout (*Oncorhynchus mykiss*) (Bromage et al., 1991). Age composition of the population and spawning experience (recruit versus repeat spawners) can also influence oocyte production (Solemdal, 1997, Atlantic cod; Marshall et al., 1998, Northeast Arctic cod; Macchi et al., 2004, Argentine hake (*Merluccius hubbsi*); Óskarsson and Taggart, 2006, Icelandic summer-spawning herring; Marteinsdottir and Begg, 2002, Atlantic cod). Changes in age and size at sexual maturation as reported in Baltic cod (Cardinale and Modin, 1999) and in the same herring stock as present (Engelhard and Heino, 2004) could also alter the reproductive potential of the stock. The NSS herring stock showed spatio-temporal segregation of early and delayed maturation individuals, both in the Norwegian and Barents Sea (Devold, 1963; Dragesund et al., 1980, 1997; Toresen and Østvedt, 2000; Engelhard and Heino, 2004).

It has been suggested that total egg production (TEP), rather than SSB, is a better measure of reproductive potential when predicting recruitment (Marshall et al., 2003), as it will account for variations in egg production as a result of fish condition, stock composition, environmental and ecological factors. The dynamics of NSS herring

reproductive output with regard to its population composition (recruit and repeat spawners abundance), structure (size and age) and condition factor have, however, not been investigated up to now. Our objective is therefore to explore the impacts of the stock structure and fish condition factor on TEP. This investigation is a contribution toward an understanding of causes for variability in recruitment, as it adds more insight to stock-recruitment relationship by incorporation of inter-annual variability in the condition of individual fish, and the size structure of the population on TEP.

The main objective is to link our knowledge of reproductive biology with stock dynamics to improve our understanding of variability in SRP, which will ultimately lead to a better understanding of processes affecting recruitment. More specifically, in this study we explored short and long-term impacts of stock fluctuations in NSS herring on perceived stock productivity, by examining total egg production at different periods and for different fish condition factors.

## **2. Materials and methods**

### *2.1. Study area and data collection*

Fishery samples caught using different gear (drift nets, beach-seines, purse-seines and trawls) and Institute of Marine Research (IMR) samples caught using research vessels were taken from NSS spawning grounds (58°N to 70°N) from 1935 to 2005. Samples of 100-200 herring per trawl station were regularly collected during the spawning months from January to March along the Norwegian coast. The latitudinal range of data may have some effect on the fish condition factor data, as condition factor may vary with latitudes (Slotte, 1999) and the sampling coverage may vary inter-annually. For each fish, standard morphometric measurements were taken: total length (TL, measured to the nearest 0.5 cm), whole body weight (W, measured to the nearest 1 gram), sex, maturity stage, as recommended in Anon. (1962), and scales were sampled for age reading. The herring included in the present analyses were all staged as maturing, i.e., in a pre-spawning state. Spawning and spent individuals were excluded from the analyses as this would have biased length weight relationships.

## 2.2. Total egg production (TEP) estimation

Input data for TEP estimation was taken from the ICES (2006) report. These data were annual spawning stock biomass (SSB) and annual spawning stock numbers (SSN) at age. Because we needed to have the data distributed over length rather than age to get the numbers at length, with their associated weight for the purposes of estimating oocyte production from the fecundity models, the total abundance was re-distributed over length. The conversion of SSB and SSN per age to length was undertaken by using the total numbers at age and then applying the length-at-age proportions given for that year in order to re-distribute the total number at age into length classes. SSN were therefore assigned to the observed proportions of 1 cm size classes in the annually derived length-age keys of mature fish on the spawning grounds. Finally, SSN by length was summed over all age groups by year, of which 50% were assumed to be females based on a relatively stable female to male ratio of 1:1 as we observed in the raw data over the whole study period to give female spawning stock number (FSSN). The annual mean weight at length was calculated using the raw data from the spawning grounds. Annual TEP was then estimated as the sum of the number of eggs produced by spawning females in each size class multiplied by their average fecundity, which was estimated from the fecundity-weight relationship given by Óskarsson et al. (2002):

$$TEP_y = \sum_{x=i}^j F_x FSSN_x ,$$

where  $y$  is year,  $x$  is size (length in cm) ranging from  $i$  to  $j$ ,  $F$  is average fecundity (number of vitellogenic oocytes per female) and FSSN is female spawning stock numbers. This method is similar to the approach used by Marshall et al. (1998). By using annual length frequencies and the year-specific length-weight relationships we were able to both utilise the fecundity-weight relationship and incorporate the effect of variable condition into the analyses (see Marshall et al. 1998). The reasoning is that fish at a given length at the onset of maturation that were heavier were in a better condition. How we obtained the parameters used in the above equation is explained in the next section.

Since we have calculated TEP from SSN, which is derived from SSB, and used the same fecundity formula in every case, we needed to investigate and verify how our modelled TEP compares with TEP estimations based on annual fecundity counts. The estimated TEP (1951-1983) from Serebryakov (1990) were compared directly with our estimates of TEP. In the case of Seliverstova (1990) fecundity at age data available for the period 1954-1975 were multiplying by the assumed number of females at age for the same years (ICES, 2006). Where fecundity data were missing for an age class a linear interpolation was used between the adjacent younger and older age classes. A further comparison was made of the annual TEP for the whole time series by replacing the equation we used from Óskarsson et al. (2002) (see above) with the weight related fecundity of Baxter (1959).

### 2.3. Fecundity (*F*) estimation

To estimate TEP of the stock it was necessary to choose an appropriate equation that best describes fecundity-length or fecundity-weight relationship of individuals, an important parameter in the TEP equation. Although there have been a number of studies on the fecundity of NSS herring (Baxter, 1959; Lyamin 1966; Seliverstova, 1990; Serebryakov, 1990; Krysov et al., 1995; Belikov et al., 1996; Ma et al., 1998; Óskarsson et al., 2002; Kurita et al., 2003; González-Vasallo, 2006), the results from Óskarsson et al. (2002) were assumed to be the most appropriate because their equation for potential fecundity was based on most recent field samples from January 1998. Their equation was  $F = 224.3 \times W - 8883$  ( $r^2=0.796$ ;  $n=47$ ), where *F* is fecundity and *W* is total body weight (g). However, it should, be noted that the fish size distribution used to determine the fecundity relationship in the work by Óskarsson et al. (2002) did not fully cover the same length and weight range as our data. Another appropriate study on NSS herring fecundity by Baxter (1959) gave both fecundity-length and fecundity-weight relationships and it was used together with that of Óskarsson et al (2002). Results of Ma et al. (1998) and González-Vasallo (2006) were based on laboratory studies and gave significantly higher relative fecundities than the other studies. The study of Kurita et al. (2003) was more concerned with atresia (resorption of oocytes) and does not give a formal equation for length or weight and fecundity. Seliverstova (1990) reported fecundity by age class rather than

with a general formula incorporating length and weight and Serebryakov (1990) reported the TEP with no fecundity formula given.

#### *2.4. Stock structure and composition*

Using the age based database, the age structure of this spawning stock was estimated for the period 1935 to 2005 by calculating the Shannon age diversity index (see Marteinsdottir and Thorarinsson, 1998 and reference therein). This index is independent of stock size, and describes both the number of cohorts contributing to the egg production and the evenness of the numbers of individuals across cohorts.

Studies on gonad development have demonstrated that length at 50% maturity in NSS herring is relatively stable at 29-30 cm for both males and females, after which all herring are repeat spawners (Østvedt, 1964; Toresen, 1986, 2001; Slotte, 1998, 1999; Óskarsson et al., 2002; Kurita et al., 2003; Engelhard and Heino, 2004). Hence, a length of 32 cm was used in the present study as a threshold between recruit (<32cm) and repeat ( $\geq 32$ cm) spawners, and it was assumed to be applicable for the whole time series under consideration.

#### *2.5. Condition factor*

The stock well-being or fitness (Bolger and Connolly, 1989) was determined as the weighted (by numbers in each length class) condition factor averaged over the 1 cm size classes each year. In this study, we used both Fulton's condition factor ( $K_F$ ) and relative condition factor ( $K_R$ ) (both referred to in Ricker, 1975). Fulton's condition factor assumes isometric growth:  $K_F = 100 \times W / TL^3$ , where  $W$  is the total weight (g) and  $TL$  is total length (cm). Relative condition factor relates the realised weight to the expected (theoretical) weight calculated from the length-weight relationship, thus  $K_R = W_R / W_{TH}$ , where  $W_R$  is realised weight in grams and  $W_{TH}$  is theoretical weight in grams.

At the population level, the average  $K$  values indicate the overall 'state' of the population's 'health'. It should be noted, however, that the condition factor of fish is influenced by the development stage of its reproductive organs (Le Cren, 1951) and



might also be length-dependent (Scott et al., 2006). Consequently, variability might be generated by individual gonad development or inter-annual variation in spawning time. The information in the database came from a number of months around spawning time; hence inter-annual variations in spawning time should not have any dramatic effect at a population scale perspective. Samples were analysed fresh on board the vessel, and therefore we assume that there were no significant effects from handling. However, to test for the possible effect of inter-annual variability, monthly average condition factor for each size class was analysed for significant differences between years. Relationships between  $K_F$  and  $K_R$  were then analysed using a continuous wavelet transform (CWT) (see Subbey et al., 2008). The wavelet approach allows a scale-to-scale comparison of the two  $K$  approaches, to see if they are in agreement. Periodicities in the condition data were analysed using Single Series Fourier Analyses in STATISTICA.

### 3. Results

#### 3.1. Population structure

Spawning stock size in biomass and in numbers as estimated by VPA indicated a decline from above  $15 \times 10^6$  tonnes or  $50 \times 10^9$  fish in 1944 and 1945 to below  $20 \times 10^3$  tonnes or  $10 \times 10^6$  fish in 1972, and again above  $8 \times 10^6$  tonnes or  $40 \times 10^9$  fish in 1997 (data from ICES, 2006, Fig. 1a). Then it has been kept at around the level of 1997. Strong recruitment to the spawning stock was evident as a significant increase in number of fish below 32 cm (Fig. 1b), with relative peaks visible during 1944, 1956, 1965, 1977, 1988, 1997 and 2004. Overall, the spawning stock was dominated (above 90%) by repeat spawners ( $\geq 32$ cm), but in the years 1943-1944, 1965-1966, 1973, 1976-1977, 1986-1989, 1996-1998 and 2003-2004 the recruit spawners were most abundant (i.e.  $> 50\%$  of the SSN) (Fig. 1b). The age structure as characterised by age diversity ( $H$ ) showed relatively large variations (Fig. 1b). Age diversity was relatively high from 1935 to the early 1950s. From then onward, through the period of stock collapse in the mid 1970s, age diversity declined. Age diversity showed a fairly rapid increase through the late 1970s to mid 1980s even though there was not a major increase in abundance. This was primarily due to an increase in number of age classes and a more even spread of ages within the stock, as the stock recovered. Large year

classes tended to make the age structure less even across year classes and this was reflected in the periodic ‘dips’ in the value of  $H$ . By the early 1990s to the present the age diversity returned to a relatively high level but not to the levels seen prior to the onset of the stock collapse.

### 3.2. Condition factor

Generally, condition variation was significant within sizes (Student  $t$ -test,  $p < 0.001$ ,  $n = 149689$ ) and between sizes (Chi-square,  $\chi^2 = 157.48$ ,  $p < 0.001$ ,  $n = 149689$ ), with more variation observed among fish that were less than 28 cm (Fig. 2). Both  $K_F$  and  $K_R$  oscillated (Fig. 3) over time, and a continuous wavelet transform showed that there was considerable similarity in fluctuations in the two measures at a wide range of inter-annual scales with the minimum correlation coefficient ( $r$ ) being approximately 0.998. This indicates that the two measures of  $K$  are in agreement and therefore any possible influence of gonad maturation did not change the condition dynamics. When the data were pooled over a 5 year moving average it appeared there was a cyclical pattern in the data (Fig. 3). Overall, the two dominant periodicities in both condition indices were 23.3 and 17.5 years for  $K_F$  and  $K_R$ , respectively (single series Fourier Analyses) (see Fig. 3). Herring reached high average conditions during the late 1950s ( $K_F = 0.85$ ), late 1970s ( $K_F = 0.86$ ) and mid 1990s ( $K_F = 0.84$ ). The lowest average  $K_F$  was observed in 1945, while the highest was observed in 1956 and 1972. During the periods toward the mid 1940s and late 1990s when abundance was at its highest (Fig. 1), there was a decrease in condition factor (Fig. 3), however, there was no significant correlation between SSN and mean condition factor ( $K_F$ ) ( $r^2 = 0.07$ ;  $P > 0.05$ ) (Fig. 4).

### 3.3. Fecundity

While fecundity estimates used here are based on a fecundity-weight relationship, Fig. 5 illustrates the potential variability in fecundity-at-length due to variability in weight-at-length or condition of the fish. The highest variation in the estimated fecundity was found among the biggest fish, possibly due to the fact that there is a tendency of more weight variation among larger fish.

### 3.4. Long-term TEP

Estimated TEP for the full time series 1935-2005 followed the SSN trend closely (Fig. 6a), but the residuals in the TEP-SSN relationships (Fig. 6b) were related to changes in proportion of recruit spawners and condition (Fig. 6c). Typically, larger deviations from this relationship were found in periods with high SSN in combination with increasing proportions of either recruit or repeat spawners and decreasing or increasing condition factor (K). Deviations were positive when the stock comprised of above 80% of repeat spawners and  $K_F$  above 0.8, and they were negative when the stock was dominated by recruit spawners (repeat spawners less than 40%, Fig. 6c) and  $K_F$  below 0.73.

### 3.5. TEP comparisons with published data sets

There existed only a few data to compare with our length-based estimate of TEP. Data from Seliverstova (1990) and Serebryakov (1990) on inter-annual variations in TEP indicate that similar levels of TEP are estimated using either Óskarsson et al.'s (2002) model or the different annually varying fecundity relationships (Fig. 7). In addition whilst there are some differences in the absolute level, especially at higher TEPs the linear regressions between different TEP estimates are highly significant ( $r^2 > 0.92$ ,  $p < 0.05$ ). The use of Baxter's (1959) fecundity relationship essentially provides the same perspective as using Óskarsson et al.'s (2002) relationship (Fig. 7).

Although linear relationships between different TEP estimated were highly significant (Fig. 8 a,b), the residual plots from both predictors (Fig. 8 c,d) showed that there were systematic deviations between the fitted curves over time, with greater differences in the 1950s, the time when the stock abundance was relatively high, and less in the 1970s, the time when the stock abundance was also decreasing substantially. Similarly, residuals against predicted values indicated that deviations were greatest during times of high predicted egg production (Fig. 8 e,f).

## 4. Discussion

In the present study, the TEP of NSS herring was estimated for the period 1935-2005 using data on population abundance and structure combined with published relationships between length, weight and fecundity. Over this 70 year period, the TEP fluctuated considerably, closely following the SSB or SSN. Residual analyses

demonstrated that positive variations in TEP that were not attributed to SSB or SSN, occurred in periods of high abundance in combination with high  $K_F$  and high proportions of repeat spawners. On the other hand, negative residuals are observed when a period of high abundance had fish with low  $K_F$  and dominated by recruit spawners. In the same periods systematic deviations were also found between the estimated TEP and previous TEP estimates (Seliverstova, 1990). This is likely to be a result of intra-annual variations in potential and relative potential fecundity in the order of 35 – 55% (Óskarsson et al., 2002), which may be a result of variation in condition factor or the composition of the stock.

The average  $K$  values should not be regarded as absolute because it is likely that intra-annual variation is influenced by gonad development, as energy reserves decline with gonad maturation (Kennedy et al., 2010). However this effect was considered minimal at the inter-annual scale because there was no statistical difference between  $K_F$  and  $K_R$ . Nevertheless, the fact that  $K_F$  and  $K_R$  indices showed similar dynamics indicates our use of Fulton's  $K$  as a reliable proxy for this stock's condition status. Patterns of changes in condition factor for the entire period could be indicating differences in allocation of energy to growth and reproduction between recruit and repeat spawners (Óskarsson et al., 2002; Engelhard and Heino, 2006). Although we have observed that most of the time  $K_F$  of the population was above 0.75, other studies (Óskarsson et al., 2002; Kennedy et al., 2010) have observed that atresia increases markedly when  $K_F$  is less than 0.7. In this regard, the long term dynamics of the state of the stock measured in condition factor would still be appropriate at the population level.

There has been variation in maturity at age and length over the years (Dragesund et al., 1980; Engelhard and Heino, 2004). Although these changes in maturity at length were relatively small, there were significant differences between year classes before, during and after the collapse (Engelhard and Heino, 2004). The year classes after the collapse (1986-2000) indicated that the stock is regaining characteristics (weight at length, and size and length at maturity) similar to those before the collapse period (1935-1968). The ICES data on age at maturity may not be accurate, because Engelhard and Heino (2004) suggested variation in spawning age that differs from that reported by in the ICES report. These changes could have led to differences in the

fecundity and productivity of the stock. In the view of the reproductive potential of recruit and repeat spawners (Slotte, 1998), changes in sexual maturation could also lead to recruitment variances when a bigger year class with early or delayed maturation is recruited. This seemed to be the case during the years that had a more skewed proportion of recruit and repeat spawners, because they correspond with the years of higher residuals. This suggests that detailed stock structure parameters are important for stock productivity and, hence, to be taken into account during assessments. Other factors like atresia (Kurita et al., 2003; Kennedy et al., 2010) and the skipped spawning (Engelhard and Heino, 2005) could also contribute to the TEP variation, but more research on these topics is required to draw any further conclusions.

The use of one weight-specific fecundity relationship to estimate TEP could have resulted in increased residuals during periods that had experienced a change in productivity due to differences in condition factors. However, the fecundity model from Óskarsson et al. (2002) was not significantly different from that of Baxter (1959), suggesting that fecundity-weight relationship in 1998 was similar to the one observed in the late 1950s. Nonetheless, levels of variations in fecundity under various conditions (González-Vasallo, 2006; Kennedy et al., 2010) can be significant, and it is therefore still advisable that fecundity and maturation schedules (maturity ogives) should be monitored frequently as there is the possibility they could change over short or long time periods. Maturation at a young but bigger size, as observed during the collapse period (Engelhard and Heino, 2005), is often associated with decline in population size (Toresen, 1990; Trippel, 1995), and could include genetic and phenotypic responses (Shin and Rochet, 1998; Olsen et al., 2004; Marshall and McAdam, 2007).

In this study we have not investigated genetic responses, but their role in changes of SRP should not be ignored. Similarly, we did not address the possibility that fecundity may increase with age for a given length or weight, or that there may be a negative effect of population cohort size on fecundity, as there is no unequivocal evidence for these phenomena in NSS herring. However, we examined the data given in Seliverstova (1990) and there was no clear trend in fecundity with age or abundance. During the time period of their investigation, mean weights were changing as was the

thermal regime, which probably confounded any potential patterns. The observed deviations between various TEPs indices illustrate other possible factors that could lead to potential different perceptions of stock productivity, as measured by total egg production. In this regard cohort based reproductive potential analyses should be considered since there are cohort effects on life history (Sæther, 1997; Beckerman et al., 2002), i.e., parental or inherited traits define individuals.

Clearly, depending on the year-specific condition factor (see e.g. Kennedy et al. 2010) and the structure of the population, total egg production of the stock can vary considerably, mostly at times of high stock abundance. For example, TEP in relation to SSN was overestimated at times when the stock was dominated by recruit spawners, and underestimated when the stock was dominated by repeat spawners. As a result, reference points derived from spawning stock biomass only, may not account for these year-specific variations and year-class structure differences. Not accounting for these factors and dynamics could lead to varying recruitment rates, and more so when coupled with environmental causes. If the egg production potential of the stock is not accounted for in stock assessments and the management, this in turn may impact on expectations for the recovery of the stock. Our work therefore suggests that quantifying the reproductive potential as TEP will contribute to understanding stock-recruitment dynamics because it captures both the population and reproductive dynamics of the stock.

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409

410 **References**

- 411 Anon., 1962. Recommendations adopted by the Herring Committee. Rapp. P.-v.  
412 Réun. Cons. Int. Explor. Mer 1, 71-73.
- 413 Bagenal, T.B., 1969. Relationship between egg size and fry survival in brown trout,  
414 *Salmo trutta* L. J. Fish Biol. 1, 349–353.
- 415 Baxter, I.G., 1959. Fecundities of winter spring and summer–autumn herring  
416 spawners. J. Cons Int. Explor. Mer 25, 73–80.
- 417 Beckerman, A.P., Benton, T.G., Ranta, E., Kaitala, V., Lundberg, P., 2002. Population  
418 dynamic consequences of delayed life-history effects. TREE 17, 263–269.
- 419 Belikov, S.V., Krysov, A.I., Seliverstova, E.I., Tereshchenko, E.S., 1996.  
420 Reproductive capacity of Norwegian spring-spawning herring during period of  
421 stock rebuilding. ICES CM 1996/H: 34.
- 422 Blanchard, J.L., Frank, K.T., Simon, J.E., 2003. Effects of condition on fecundity and  
423 total egg production of eastern Scotian Shelf haddock. Can. J. Fish. Aquat. Sci., 60,  
424 321–332.
- 425 Bolger, T., Connolly, P.L., 1989. The selection of suitable indices for the  
426 measurement and analysis of fish condition. J. Fish Biol. 34, 171–182.
- 427 Bromage, N.R., Jones, J., Randall, C., Thrush, M., Springate, J., Duston, J., Barker,  
428 G., 1991. Broodstock management, fecundity, egg quality and the timing of egg  
429 production in the rainbow trout (*Oncorhynchus mykiss*). Aquaculture 100, 141–166.
- 430 Cardinale, M., Modin, J., 1999. Changes in size-at-maturity of Baltic cod (*Gadus*  
431 *morhua*) during a period of large variations in stock size and environmental  
432 conditions. Fish. Res. 41, 282-295.
- 433 Devold, F., 1963. The life history of the Atlanto-Scandian herring. Rapp. P.-v. Réun.  
434 Cons. Int. Explor. Mer 154, 98–108.
- 435 Dragesund, O., Hamre, J., Ulltang, Ø., 1980. Biology and population dynamics of the  
436 Norwegian spring-spawning herring. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 177,  
437 43–71.
- 438 Dragesund, O., Johannessen, A., Ulltang, Ø., 1997. Variation in migration and  
439 abundance of Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia 82,  
440 97–105.

Engelhard, G.H., Heino, M., 2004. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. *Fish. Res.* 66, 299–310.

Engelhard, G.H., Heino, M., 2005. Scale analysis suggests frequent skipping of the second reproductive season in Atlantic herring. *Biol. Lett.* 1, 172–175.

Engelhard, G.H., Heino, M., 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. *Oecologia* 149, 593–603.

González–Vasallo, B.D., 2006. Regulatory reproductive mechanisms and somatic growth in Atlantic herring (*Clupea harengus* L.). M.Sc. thesis, Department of Biology, University of Bergen, Bergen, Norway.

Hislop, J.R.G., Robb, A.P., Gauld, J.A., 1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.), in captivity. *J. Fish Biol.*, 13, 85–98.

Holst, J.C., Røttingen, I., Melle, W. 2004. The herring. *In*: H.R. Skjoldal, R. Sætre, A. Færnø, O.A. Misund, I. Røttingen (eds.) *The Norwegian Ecosystem*. Tapir Academic Press, Trondheim, Norway. pp 203–226.

ICES, 1999. Report of the northern pelagic and blue whiting fisheries Working Group. ICES CM 1999/ACFM:18.

ICES, 2006. Report of the northern pelagic and blue whiting fisheries Working Group (WGNPBW). ICES CM 2006/ACFM:34. 294pp.

ICES, 2007. Report of the northern pelagic and blue whiting fisheries Working Group (WGNPBW). ICES CM 2007/ACFM:29. 226pp.

Kennedy, J., Skjæraasen, J.E., Nash, R.D.M., Thorsen, A., Slotte, A., Hansen, T., Kjesbu, O.S., 2010. Do capital breeders like Atlantic herring (*Clupea harengus* L.) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? *Can. J. Fish. Aquat. Sci.* 67, 16–27.

Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R., Greer Walker, M.G., 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Can. J. Fish. Aquat. Sci.* 48, 2333–2343.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., Greer Walker, M., 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J. Sea Res.* 40, 303–321.



474 Klibansky, N., Juanes, F., 2008. Procedures for efficiently producing high-quality  
 475 fecundity data on a small budget. *Fish. Res.* 89, 84–89.

476 Krysov, A. I., Seliverstova, E. I., Tereshchenko, E. S., 1995. Stock status and  
 477 dynamics of Norwegian spring-spawning herring fecundity in 80-S. *In*: T. Monstad  
 478 (ed.). *Proceedings of the Fourth Soviet–Norwegian Symposium*, Bergen, 12–16  
 479 June 1989. Institute of Marine Research, Bergen. pp. 264–271.

480 Kurita, Y., Meier, S., Kjesbu, O.S., 2003. Oocyte growth and fecundity regulation by  
 481 atresia of Atlantic herring (*Clupea harengus*) in relation to body condition  
 482 throughout the maturation cycle. *J. Sea Res.* 49, 203–219.

483 Lambert, Y., Dutil, J.-D., 2000. Energetic consequences of reproduction in Atlantic  
 484 cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Can.*  
 485 *J. Fish. Aquat. Sci.* 57, 815–825.

486 Lambert, Y., Yaragina, N.A., Kraus, G., Marteinsdottir, G., Wright, P.J., 2003. Using  
 487 environmental and biological indices as proxies for egg and larval production of  
 488 marine fish. *J. Northwest Atl. Fish. Sci.* 33, 115–159.

489 Le Cren, E.D., 1951. Length-weight relationship and seasonal cycle in gonad weight  
 490 and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20, 201–219.

491 Lyamin, K.A., 1966. Fecundity of the spring race of Atlanto–Scandian herring. *Trudy*  
 492 *PINRO* 17, 147–192 (In Russian).

493 Ma, Y., Kjesbu, O.S., Jørgensen, T., 1998. Effects of ration on the maturation and  
 494 fecundity in captive Atlantic herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.*  
 495 55, 900–908.

496 Macchi, G.J., Pajaro, M., Ehrlich, M., 2004. Seasonal egg production pattern of the  
 497 Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish. Res.* 67, 25–38.

498 Marshall, C.T., McAdam, B.J., 2007. Integrated perspectives on genetic and  
 499 environmental effects on maturation can reduce the potential for errors of inference.  
 500 *Mar. Ecol. Prog. Ser.* 335, 301–310.

501 Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., Ulltang, Ø., 1998. Is  
 502 spawner biomass a sensitive measure of the reproductive and recruitment potential  
 503 of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* 55, 1766–1783.

504 Marshall, C.T., Yaragina, N.A., Ådlandsvik, B., Dolgov, A.V., 2000. Reconstructing  
 505 the stock–recruit relationship for Northeast Arctic cod using a bioenergetic index of  
 506 reproductive potential. *Can. J. Fish. Aquat. Sci.* 57, 2433–2442.

507 Marshall, C.T., O'Brien, L., Tomkiewicz, J., Marteinsdottir, G., Morgan, M.J.,  
 508 Saborido-Rey, F., Köster, F.W., Blanchard, J.L., Secor, D.H., Kraus, G., Wright,  
 509 P.J., Mukhina, N.V., Björnsson, H., 2003. Developing alternative indices of  
 510 reproductive potential for use in fisheries management: case studies for stocks  
 511 spanning an information gradient. J. Northwest Atl. Fish. Sci. 33, 161–190.  
 512 Marteinsdottir, G., Begg, G.A., 2002. Essential relationships incorporating the  
 513 influence of age, size and condition on variables required for estimation of  
 514 reproductive potential in Atlantic cod, *Gadus morhua*. Mar. Ecol. Prog. Ser. 235,  
 515 235–256.  
 516 Marteinsdottir, G., Thorarinsson, K., 1998. Improving the stock-recruitment  
 517 relationship in Icelandic cod (*Gadus morhua*) by including age diversity of  
 518 spawners. Can. J. Fish. Aquat. Sci. 55, 1372–1377.  
 519 Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P. R., Thorsen, A., Junquera, S.,  
 520 2003. Procedures to estimate fecundity of marine fish species in relation to their  
 521 reproductive strategy. J. Northwest Atl. Fish. Sci. 33, 33–54.  
 522 Nakken, O. (Ed.), 2008. Norwegian Spring-Spawning Herring & Northeast Arctic  
 523 Cod. 100 Years of Research and Management. Tapir Academic Press, Trondheim.  
 524 177pp.  
 525 Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B.,  
 526 Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the  
 527 collapse of northern cod. Nature 428, 932–935.  
 528 Óskarsson, G.J., Taggart, C.T., 2006. Fecundity variation in Icelandic summer-  
 529 spawning herring and implications for reproductive potential. ICES J. Mar. Sci., 63,  
 530 493–503.  
 531 Óskarsson, G.J., Kjesbu, O.S., Slotte, A. 2002. Predictions of realized fecundity and  
 532 spawning time in Norwegian spring-spawning herring (*Clupea harengus*). J. Sea  
 533 Res. 48, 59–79. Østvedt, O.J., 1964. Comparison between catch per unit effort in the  
 534 Norwegian gill net and purse seine fishery for herring. Rapp. P.-v. Réun. Cons. Int.  
 535 Explor. Mer 155, 90–93.  
 536 Ricker, W.E., 1975. Computation and Interpretation of Biological Statistics of Fish  
 537 Populations. Bull. Fish. Res. Board Can. 191.  
 538 Rijnsdorp, A.D., 1991. Changes in fecundity of female North Sea plaice  
 539 (*Pleuronectes platessa* L.) between three periods since 1900. ICES J. Mar. Sci. 48,  
 540 253–280.

541 Scott, B.E., Marteinsdottir, G., Wright, P., Kjesbu, O.S., 2006. Effects of population  
542 structure, condition and temporal dynamics of flexible life history traits on  
543 reproductive output in Atlantic cod (*Gadus morhua*). Ecol. Model. 191, 383-415.

544 Seliverstova, E.I., 1990. Spawning stock structure and population fecundity of the  
545 Atlanto-Scandian herring. In: T. Monstad (ed.). Proceedings of the Fourth Soviet–  
546 Norwegian Symposium, Bergen, 12–16 June 1989. Institute of Marine Research,  
547 Bergen. pp. 41-88.

548 Serebryakov, V.P., 1990. Population fecundity and reproductive capacity of some  
549 food fishes in relation to year-class strength fluctuations. J. Cons. Int. Explor. Mer  
550 47, 267-272.

551 Shin. Y.-J., Rochet. M.-J., 1998. A model for the phenotypic plasticity of North Sea  
552 herring growth in relation to trophic conditions. Aquat. Liv. Resour. 11, 315–324.

553 Skjæraasen, J.E., Nilsen, T., Kjesbu, O.S., 2006. Timing and determination of  
554 potential fecundity in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 63,  
555 310–320.

556 Slotte, A., 1998. Spawning migration of Norwegian spring spawning herring (*Clupea*  
557 *harengus* L.) in relation to population structure. Dr. Sci. thesis, Department of  
558 Fisheries and Marine Biology, University of Bergen, Bergen, Norway.

559 Slotte, A., 1999. Effects of fish length and condition on spawning migration in  
560 Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia 84, 111–127.

561 Solemdal, P., 1997. Maternal effects – a link between the past and the future. J. Sea  
562 Res. 37, 213–227.

563 Subbey, S., Michalsen, K., Nilsen, G.K., 2008 A tool for analyzing information from  
564 data storage tags: the continuous wavelet transform (CWT). Rev. Fish Biol. Fish.  
565 18, 301-312.

566 Sæther, B.E., 1997. Environmental stochasticity and population dynamics of large  
567 herbivores: a search for mechanisms. TREE 12, 143–149.

568 Toresen, R., 1986. Length and age at maturity of Norwegian spring spawning herring  
569 for the year classes 1959-61 and 1973-78. ICES CM 1986/H: 42.

570 Toresen, R., 1990. Long-term changes of growth and maturation in the Norwegian  
571 spring spawning herring. In: Monstad, T., (ed.), Biology and Fisheries of the  
572 Norwegian Spring Spawning Herring and Blue Whiting in the Northeast Atlantic.  
573 Institute of Marine Research, Bergen, Norway. pp. 89-106.

574 Toresen, R., 2001. Environmental influences on herring (*Clupea harengus* L.)  
 575 abundance: an environmental approach for the understanding of herring stock  
 576 fluctuations and its application in management. Dr. phil. thesis, University of  
 577 Bergen, Bergen, Norway.  
 578 Toresen, R., Østvedt, O.J., 2000. Variation in abundance of Norwegian spring  
 579 spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and  
 580 the influence of climatic fluctuations. Fish Fish. 1, 231–256.  
 581 Toresen, R., Østvedt, O.J., 2002. Stock structure of Norwegian spring-spawning  
 582 herring: historical background and recent apprehension. ICES Mar. Sci. Symp. 215,  
 583 532-542.  
 584 Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45,  
 585 759–771.  
 586 Trippel, E.A., 1998. Egg size and viability and seasonal offspring production of young  
 587 Atlantic cod. Trans. Am. Fish. Soc. 127, 339–359.  
 588 Trippel, E.A., 1999. Estimation of stock reproductive potential: history and challenges  
 589 for Canadian Atlantic gadoid stock assessments. J. Northw. Atl. Fish. Sci. 25, 61–  
 590 81.  
 591 Tyler, A.V., Dunn, R.S., 1976. Ration, growth, measures of somatic and organ  
 592 condition in relation to meal frequency in winter flounder (*Pseudopleuronectes*  
 593 *americanus*), with hypotheses regarding population homeostasis. J. Fish. Res.  
 594 Board Can. 33, 63–75.  
 595

**Fig. 1.** Norwegian spring-spawning herring population abundance and structure over the period 1935 to 2005. (a) annual spawning stock size in numbers (SSN, bars) and spawning stock biomass (SSB, line), (b) the stock structure per recruit ( $< 32$  cm, black bars) and repeat spawners ( $\geq 32$  cm, grey bars) and Shannon age diversity index  $H$  (line).

**Fig. 2.** The variability (mean  $\pm$  range) in Fulton's condition factor ( $K_F$ ) and relative condition factor ( $K_R$ ) over the range of length classes in Norwegian spring-spawning herring. Each data point represents the mean and standard deviation (SD) of observed fish at each length over time.

**Fig. 3.** Annual variations of the Norwegian spring-spawning herring  $K_F$  and  $K_R$  (mean  $\pm 0.95$  confidence limits) together with the weighted condition factor and a five years moving average.

**Fig. 4.** Relationship between  $K_F$  and SSN for Norwegian spring-spawning herring.

**Fig. 5.** The variability in fecundity over the range of mature length classes in Norwegian spring-spawning herring. Óskarsson et al. (2002) (open squares) and Baxter (1959) (filled squares). Fecundity relationship of Óskarsson et al. (2002) is a function of weight but transformed to length, using weight-length relationship. Each data point represents the mean and standard deviation (SD) of observed fish at each length over time.

**Fig. 6.** (a) annual TEP (solid line and dash-dotted line), SSB, (dashed line), and SSN (dotted line), (b) TEP against SSN residuals over time and (c) the relationship between the proportion of repeat spawners,  $K_F$  and the annual residuals from TEP-SSN for the years corresponding to the residuals. Closed circles represent annual residuals at their corresponding annual proportions of repeat spawners and each open square represent average  $K_F$ .

**Fig. 7.** (a) total egg production over time as estimated by different authors (Óskarsson et al, solid line: Baxter, dash-dotted line; Serebryakov, dotted line and Seliverstova, mesh line)..

**Fig. 8.** Relationship between various TEP estimates (a, b) and the residuals by year (c, d) or TEP (e, f), between this study (based on the fecundity curve of Óskarsson et al. (2002)) and Seliverstova (1990) and Serebryakov (1990).

Figure 1

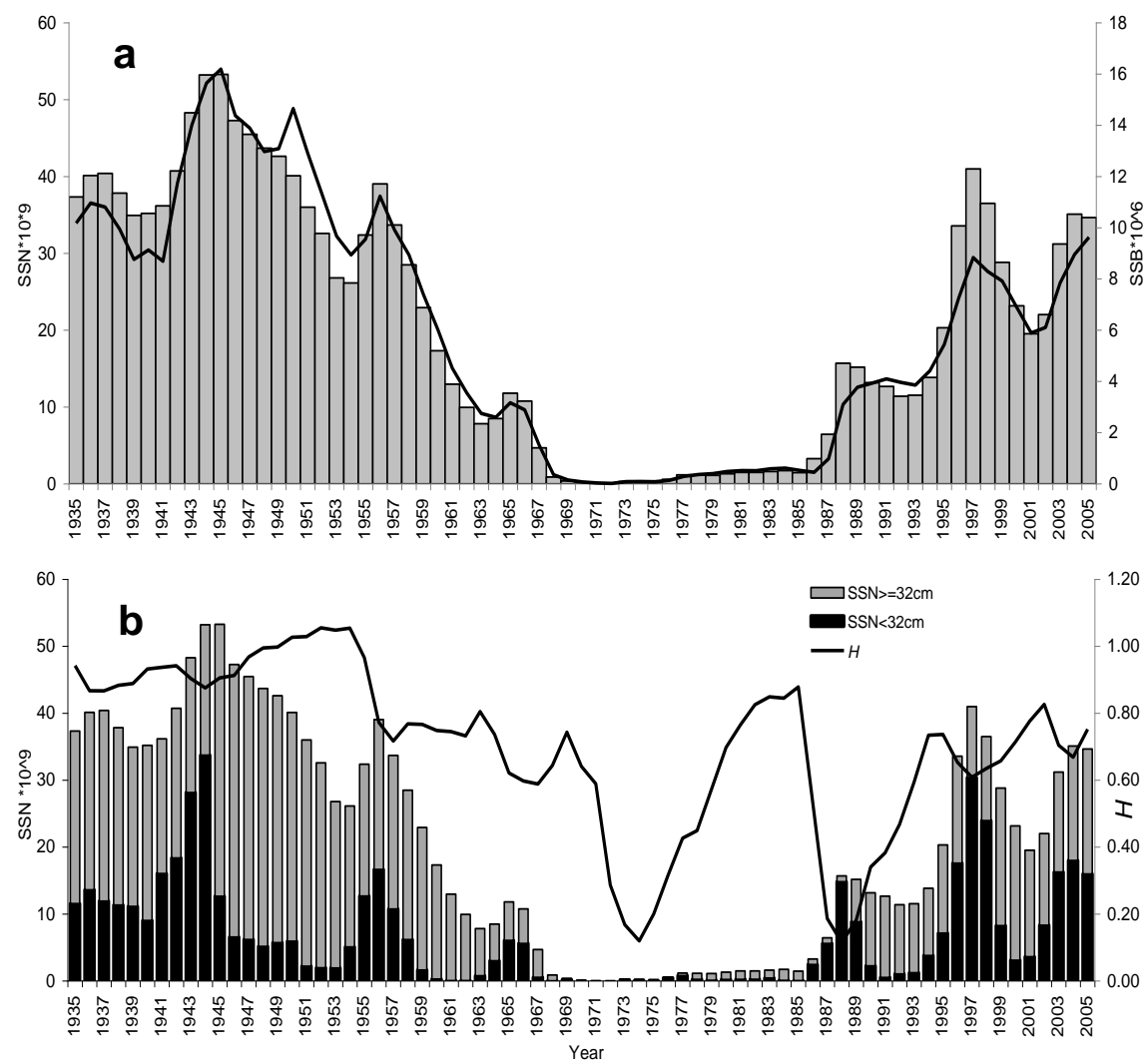


Figure 2

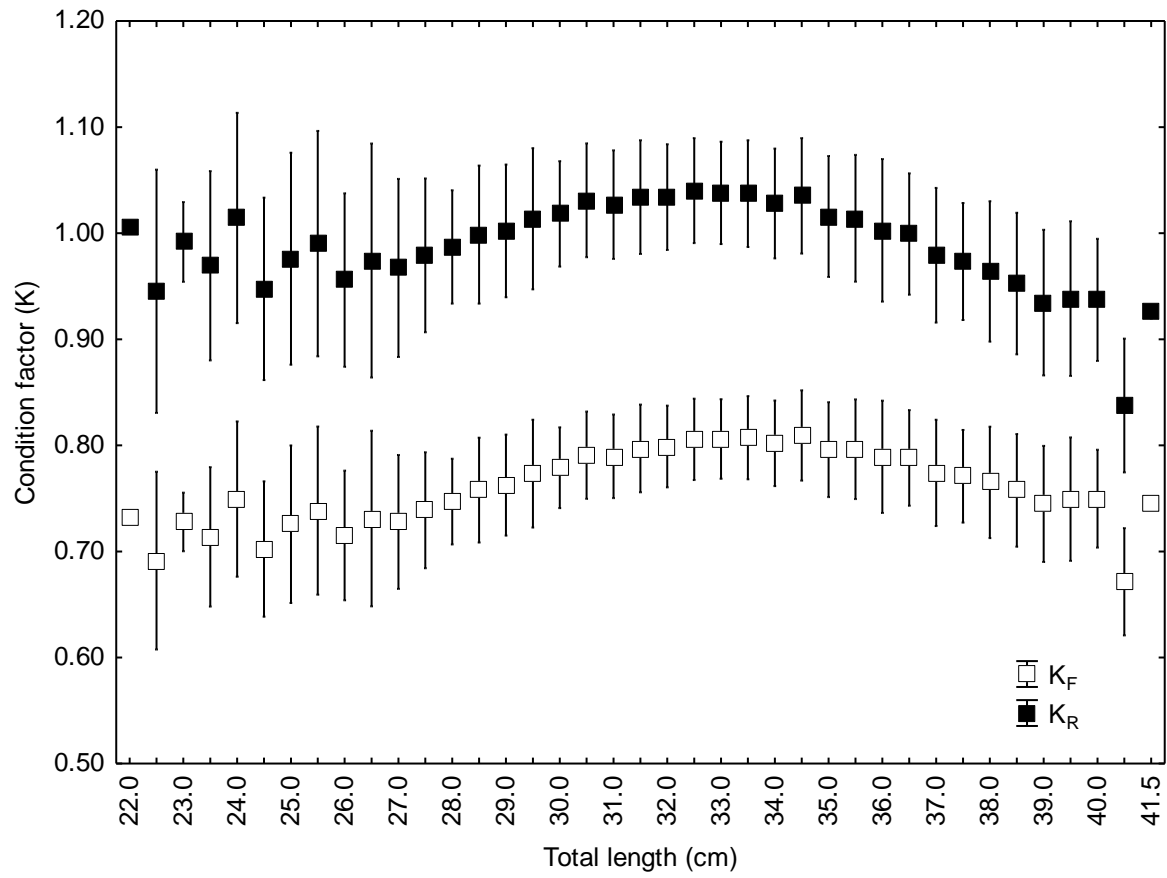




Figure 3

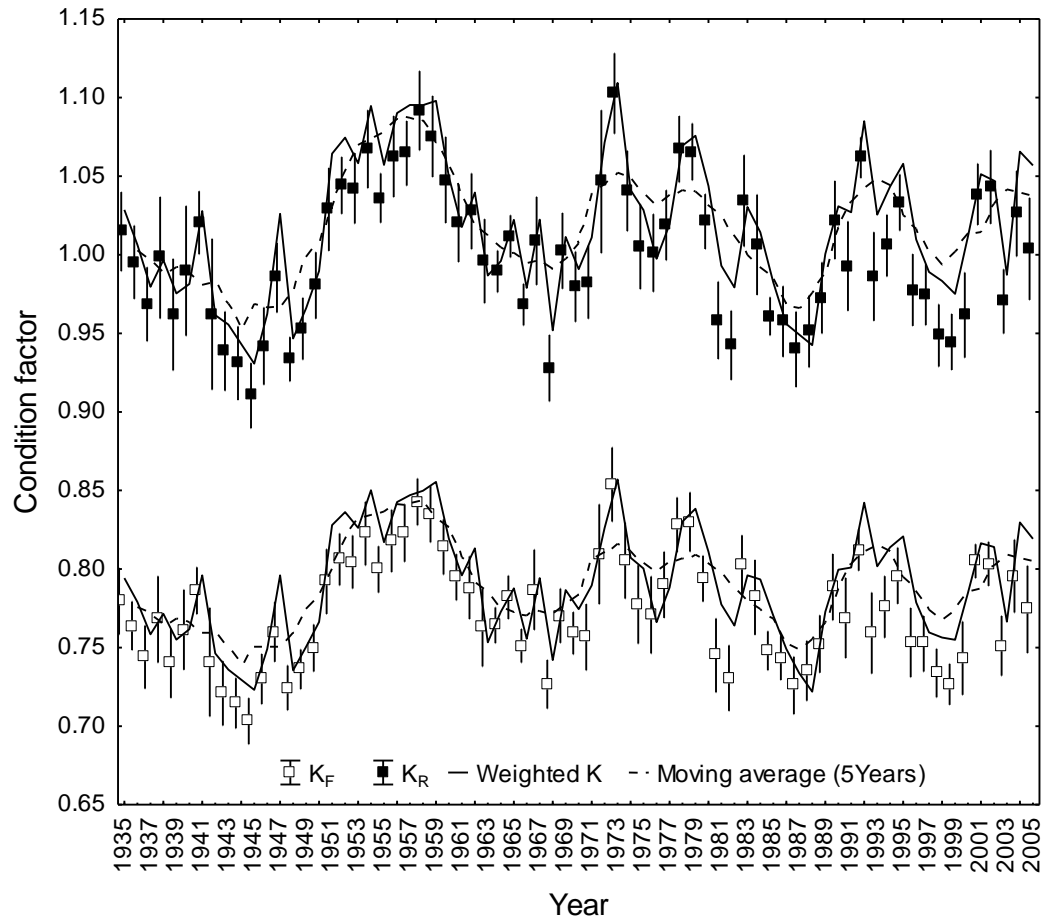


Figure 4

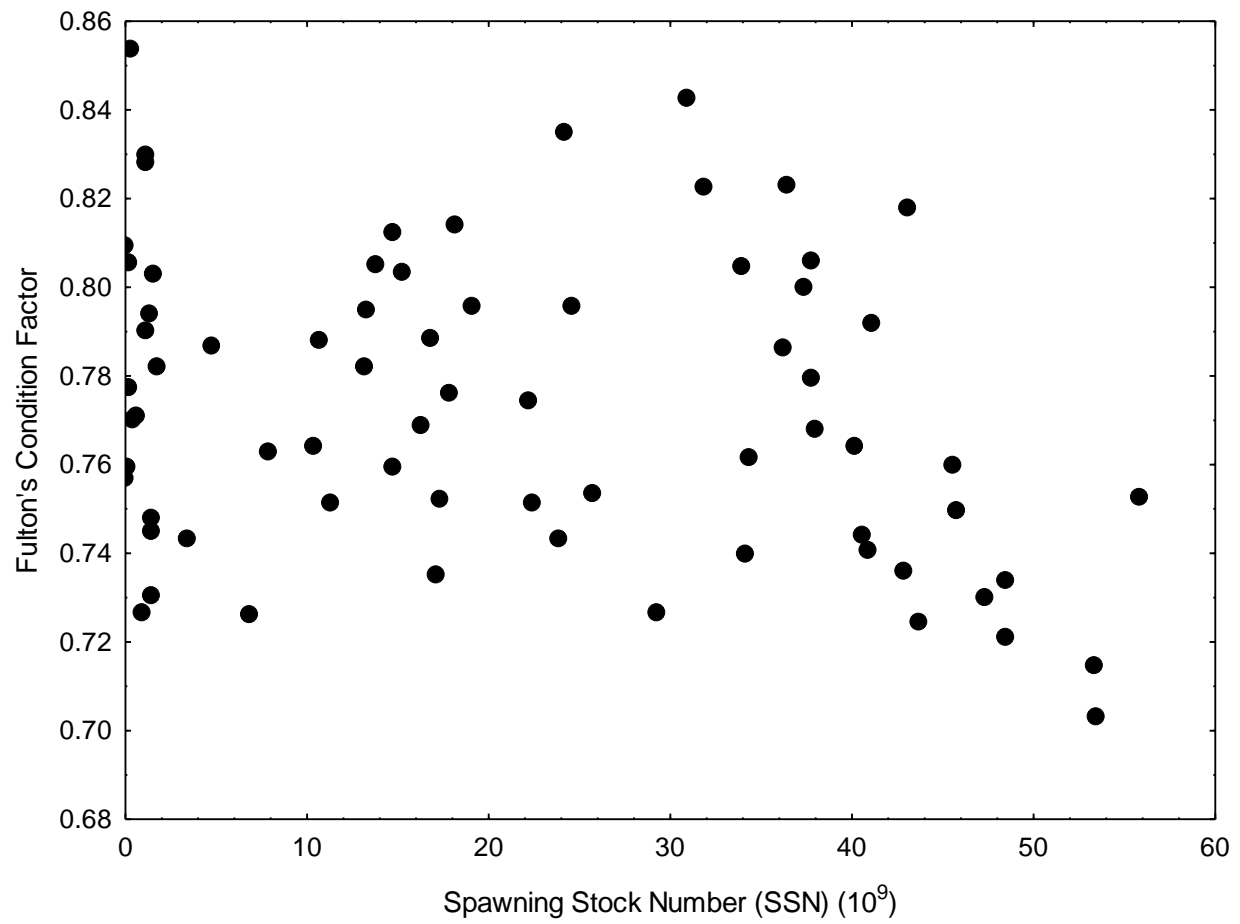


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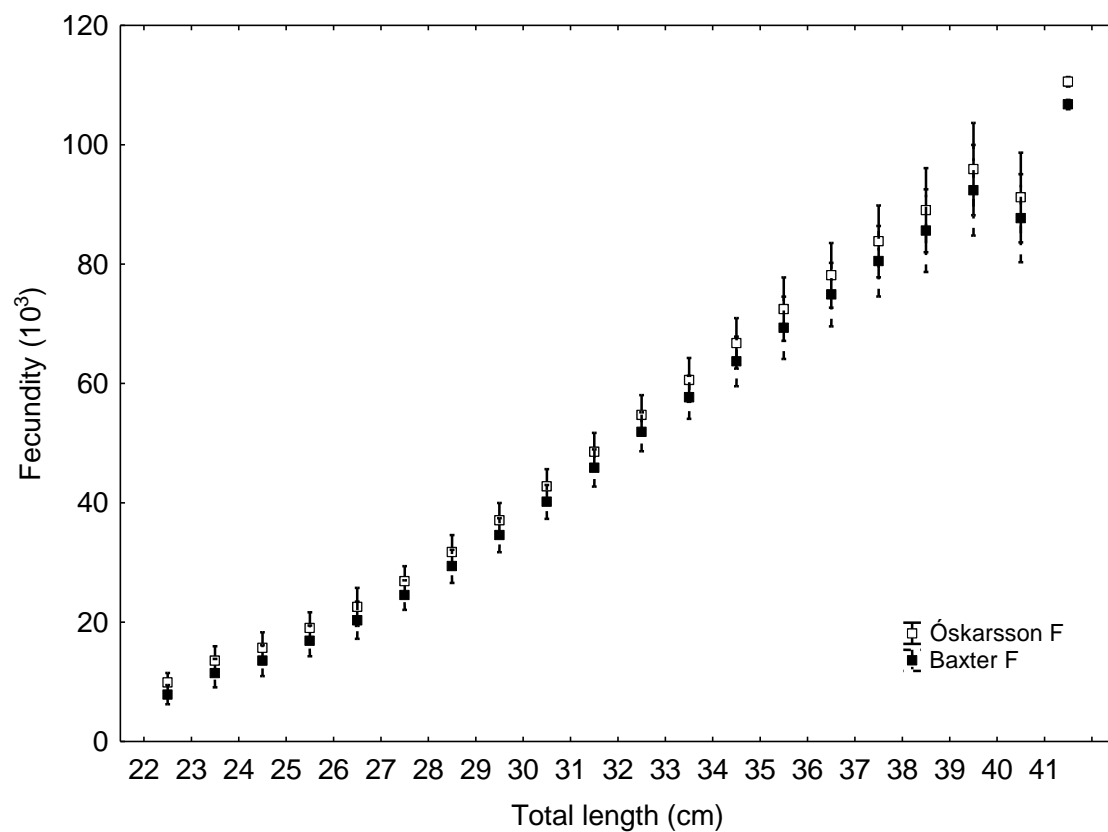


Figure 6.

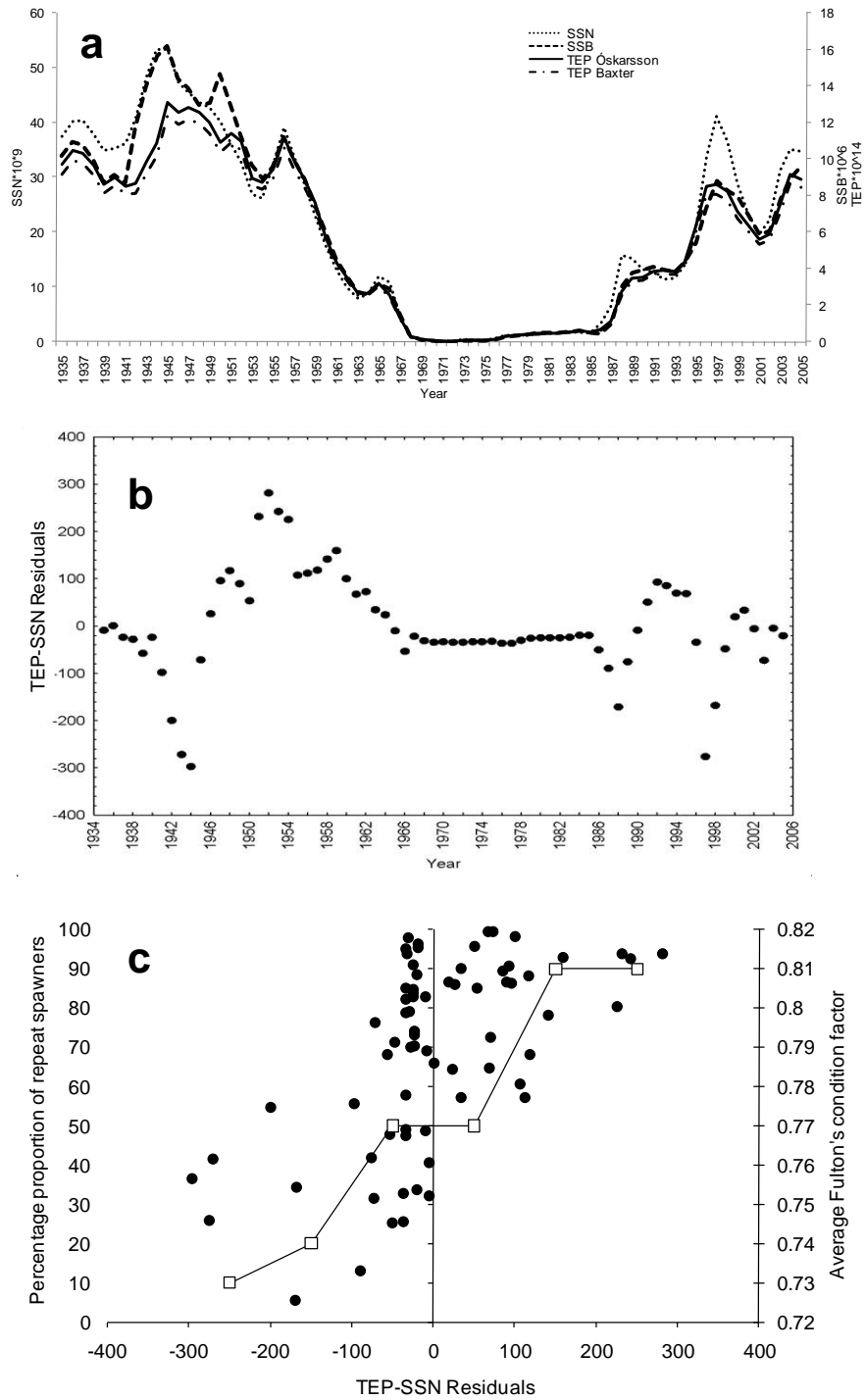


Figure 7.

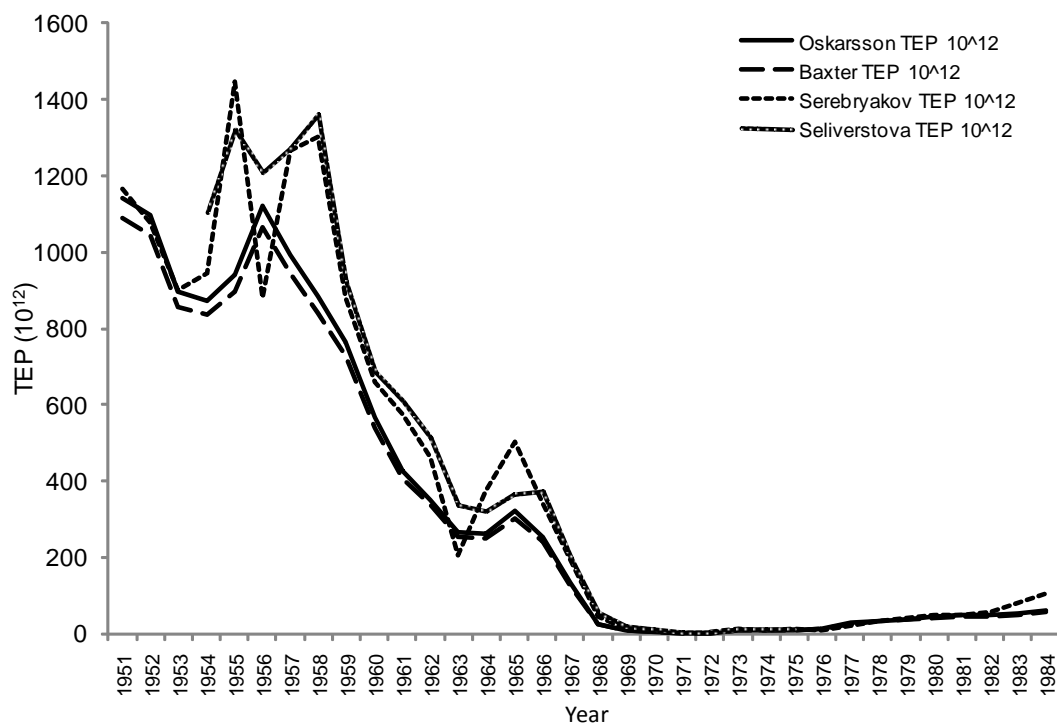


Figure 8.

